Fish Physiology and Biochemistry **19:** 189–196, 1998.
© 1998 *Kluwer Academic Publishers. Printed in the Netherlands.*

Physiological and behavioral responses to hypoxia in the bonnethead shark, *Sphyrna tiburo*: routine swimming and respiratory regulation

G.R. Parsons and J.K. Carlson*
*Department of Biology, The University of Mississippi, University, MS 38677, USA (Phone: 601-232-7479; Fax: 601-232-5144; E-mail: bygrp@olemiss.edu); *Present address: National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 3500 Delwood Beach Rd., Panama City, FL 32408, USA*

Accepted: January 23, 1998

Key words: hypoxia, shark swimming, respiration rate, mouth gape

Abstract

We examined the effect of hypoxia on the swimming speed, respiration rate (oxygen uptake), gape and ventilation volume of the bonnethead shark, *Sphyrna tiburo*. We used a sonic flowmeter developed for this study to examine swimming speed changes of sharks held in artificial lagoons during diurnal dissolved oxygen changes. Sharks were observed to swim at about 34 cm s^{-1} during the day but increased to about 40 cm s^{-1} at night when dissolved oxygen levels fell to < 3 mg l^{-1}. Using a closed system respirometer we examined changes in swimming speed, respiration rate and gape at four dissolved oxygen levels. Swimming speeds averaged 24 to 25 cm s^{-1} under normoxic conditions but increased to 38 to 40 cm s^{-1} during hypoxia. Similarly, respiration rate increased with increasing speed and decreasing dissolved oxygen. Gape averaged about 1.0 cm under normoxic conditions and increased to a maximum of about 3.5 cm during hypoxia. Using assumed oxygen extraction efficiencies of 25, 50 and 75% and observed respiration rates, we estimated that ventilation volumes of about 25 to 470 l h^{-1}, depending upon oxygen concentration, would be necessary for gill ventilation. These experiments suggest that changes in swimming speed and mouth gape are important for respiratory regulation in ram ventilating sharks.

Introduction

Changes in environmental oxygen concentration may have profound effects on the behavior, physiology and distribution of fishes. However, oxygen concentration and its effect on swimming in the ram ventilating fishes (sharks, tuna, mackerel, etc.) has not been widely examined. These fish have lost the buccal pumping mechanism and must maintain constant forward movement for gill ventilation. The requirement for continuous activity makes these fish behaviorally and physiologically unique, but, likewise, makes them difficult research subjects.

Apparently, there are species specific differences in response to hypoxia among the ram ventilating fishes. In some cases, environmental change, such as hypoxia, may not affect swimming speed in continuously active, ram-ventilating fishes (Magnuson 1973; Dizon et al. 1977). Magnuson (1978) reported that several scombrid species maintained constant swimming speed despite changes in time of day, dissolved oxygen concentration, water temperature, and degree of food deprivation. However, an increase in swimming speed in response to hypoxia has been observed in some species. Dizon (1977) reported that hypoxia elicited an increase in swimming speed in skipjack tuna, *Katsuwonus pelamis*, but did not in yellowfin tuna, *Thunnus albacares.* Bushnell and Brill (1991) reported increases in swimming speed in both *K. pelamis* and *T. albacares* in response to hypoxia.

The effect of hypoxia on elasmobranch behavior and physiology has been restricted to a few studies on species that are not obligate ram-ventilators (Randall 1970; Metcalf and Butler 1984). In this study, we used a sonic flowmeter to examine *in situ* swimming speeds of the ram-ventilating bonnethead shark, *Sphyrna tiburo* during diurnal changes in oxygen concentration. Additionally, we used closed system

respirometry to examine hypoxia induced changes in swimming speed, gape, and respiration rate (oxygen uptake). Finally, we calculated ventilation volumes over a range of dissolved oxygen concentrations and gill extraction efficiencies.

Materials and methods

In situ *swimming speeds*

Swimming speeds of captive *S. tiburo* were monitored at the Keys Regional Marine Lab, in Layton, Florida. The sharks were captured by hook and line from Florida Bay, held in captivity for about 10 days and were feeding well. Sharks were held in artificial lagoons measuring approximately 1.0 meter maximum depth, 10 meters width and 30 meters length. Water was pumped directly from Florida Bay and slowly circulated through the lagoons with no detectable current. During swimming speed determinations, temperature and dissolved oxygen were measured once per hour for a 24 h period.

A sonic tag (Figure 1) was attached to the sharks through the dorsal fin and swimming speed monitoring was begun 8 h later. The body of the tag was constructed of PVC pipe and consisted of a propeller connected to a rotating shaft with a magnet attached. The rotating magnet opened and closed a reed switch and thus turned a small 4.2 kHz transmitter off and on. Power for the transmitter was supplied by a battery pack containing four, three volt, watch batteries. The tag weighed 52.8 g in air and 20.5 g in seawater and was approximately 11.0 cm long and 3.4 cm wide (Figure 1). Details of the construction of the sonic tag are available from the primary author. The tag was attached to the shark such that the propeller was positioned just ahead of the first dorsal fin and was in free-stream flow. The pulsed signal was recorded with a hydrophone and cassette recorder for later analysis.

Prior to attaching the tag to the sharks, the signal from the tag was calibrated by determining the pulse rate at various current speeds using a Marsh-McBirney flowmeter and a Brett type water tunnel. Calibration of the tag was accomplished using the mid-body section, with attached dorsal fin, removed from a freshly sacrificed shark. The tag was attached to the dorsal fin and the mid-body section was placed in the water tunnel with the tag directed up current. Pulse rate of the sonic tag was determined over a range of flow speeds. Flow speeds during calibration were corrected for solid blocking according to Smit et al. (1971).

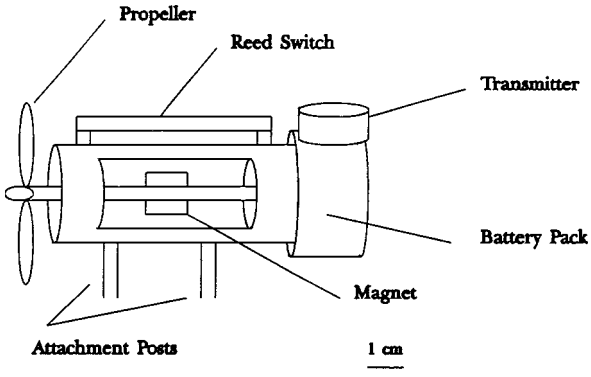

Figure 1. A diagram of the sonic flowmeter used for the study.

Respirometry

Respirometry experiments were conducted at the National Marine Fisheries Service Laboratory in Panama City, Florida. Sharks were captured from St. Andrews Bay, Florida using gill nets and transported to the laboratory. Sharks were held for up to 1 month in outdoor shaded, circular 4000-l tanks with flowing seawater. Sharks used in experiments were feeding well and exhibited no signs of poor health. Prior to experimentation sharks were not fed for up to 96 h to achieve a postabsorptive state.

To examine changes in behavioral and physiological parameters in response to hypoxia, a closed system, circular, respirometer (inner diameter 182 cm $\times$ depth 58 cm) was constructed using a 1500-l polyethylene tank. The tank was permanently sealed using silicon sealant and a plywood and plexiglas lid. Plexiglas windows cut into the sides and top of the respirometer allowed for behavioral observations during experiments. A removable window in the top of the tank allowed sharks to be placed in the respirometer.

The experiment began by filling the respirometer with filtered and UV sterilized seawater at 30 ppt salinity and 19($\pm$2) °C temperature. We placed a shark in the respirometer and following Parsons (1990) allowed the shark to acclimate for 24 h. Continuous aeration was provided during acclimation. After the acclimation period, aeration ceased and the respirometer was sealed. A polarographic oxygen electrode was inserted into the respirometer and connected to an amplifier and Linseis chart recorder for continuous dissolved oxygen recording. During the experiment, sharks swam continuously around the outer edge which provided mixing of water. Preceding and immediately after each experiment, oxygen concentration was verified using a YSI Model 51B oxygen meter.

Behavioral and physiological measurements (e.g., swim speed, gape, respiration rate) were taken every 30 to 60 minutes. Swimming speed (cm s^{-1}) was measured by noting the time required for the shark to pass between two points of known distance marked on the respirometer. Gape was measured to the nearest 0.5 cm by directly comparing gape to a vertical scale present on the window and from photographs of the shark taken through the window of the respirometer using a 35 mm camera. Respiration rate was calculated using the general equation:

$$VO_2 = bsv/w$$

where VO_2 is respiration rate in mg O_2 kg^{-1} h^{-1}, b is the rate of change of oxygen in the respirometer, s is the solubility of oxygen calculated at the experimental temperature and pressure, v is the volume of the respirometer and w is the wet weight of the shark. When dissolved oxygen concentrations reached between 2.5 and 3.0 mg l^{-1}, the seal was broken on the tank and aeration begun. In some experiments, we continued to monitor gape and swimming speed during the return to normoxia (5.5–5.6 mg l^{-1}). At the end of the experiment the shark was removed from the respirometer, weighed (kg $\pm$ 0.01), total length measured (cm $\pm$ 0.1) and returned to the holding tank. No sharks died as a result of these experiments and all were later released.

Experiments and controls were conducted under constant light to eliminate variation in external cues that might influence swimming speed. To insure that the hypoxia effect would not be confused with any endogenous activity pattern that might exist, we conducted experiments at all times of the day and night such that hypoxic conditions never consistently coincided with a particular time of day. The water in the respirometer was replaced after 24 h of use and no significant background respiration was measured when the experiment was conducted minus the shark.

For data analysis, dissolved oxygen was grouped into four treatment levels, 3, 4, 5 and 6 ($\pm$ 0.5) mg l^{-1} oxygen. The average of all replicate measurements within each level were determined for each individual shark. Consequently, the mean for each shark at each oxygen treatment level was compared using a repeated measures analysis of variance with post hoc tests. Regression was used to examine the effect of dissolved oxygen on respiration rate.

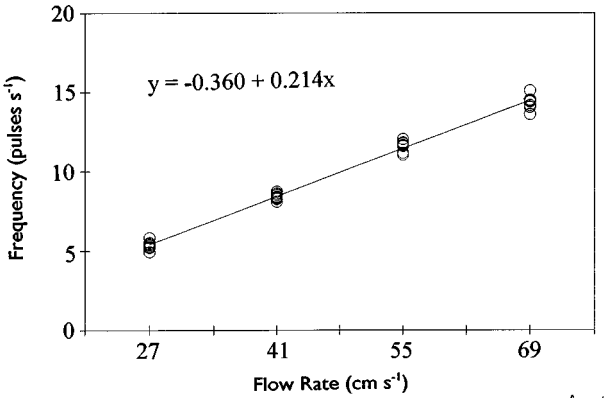

Figure 2. A linear regression of the relationship between flow rate and signal frequency for the sonic flowmeter (r = 0.996).

Results

In situ *swimming speeds*

A linear relationship was observed between pulse rate of the sonic tag and current speed (Figure 2). The signal from the tag varied from about 5 pulses s^{-1} at 27 cm s^{-1} flow rate to about 15 pulses s^{-1} at 69 cm s^{-1}. There was no problem with the tag becoming fouled.

Swimming speed was monitored over a 24 h period (Figure 3) on 29 July and 5 August, 1991 using two different female sharks of similar lengths (95 and 99 cm total length, 4.2 and 5.5 kg mass). Swimming speeds were lowest during the day averaging 34.3 ($\pm$ 2.5 SD) and 35.9 ($\pm$ 2.1 SD) cm s^{-1}, respectively. Swimming speeds during the night averaged 38.3 ($\pm$ 2.0 SD) and 39.6 ($\pm$ 0.8 SD) cm s^{-1}, respectively. Student's t-test revealed that swimming speeds at night were significantly greater (p = 0.014 and 0.003 for 29 July and 5 August, respectively) than those recorded during the day. There was also observed a crepuscular increase in swimming speed immediately after sunrise and sunset (Figure 3). Swimming speed decreased almost linearly throughout the morning hours with lowest speeds recorded between 1200 and 2000 h. Temperature of the lagoon varied little during swimming speed observations ranging from about 30 °C at night to about 33.5 °C during the day. However, dissolved oxygen changes were extreme decreasing to a minimum of 2.6 mg l^{-1} at 0500 h and increasing to a maximum of 6.0 mg l^{-1} at 1700 h.

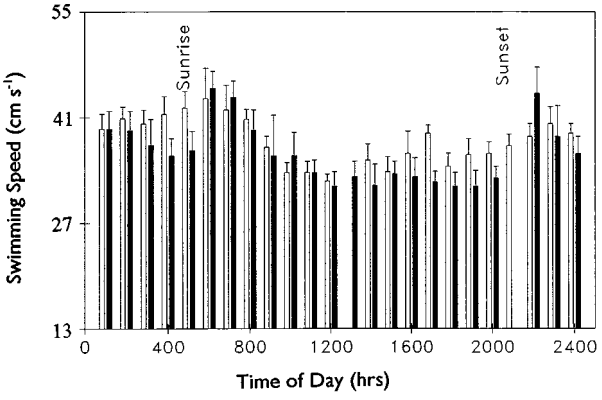

Figure 3. Swimming speeds of *S. tiburo* monitored over 24 hour periods. The means and standard deviations are shown for each hour. The filled histogram represents speeds recorded on 29 July and the open histogram on 5 August.

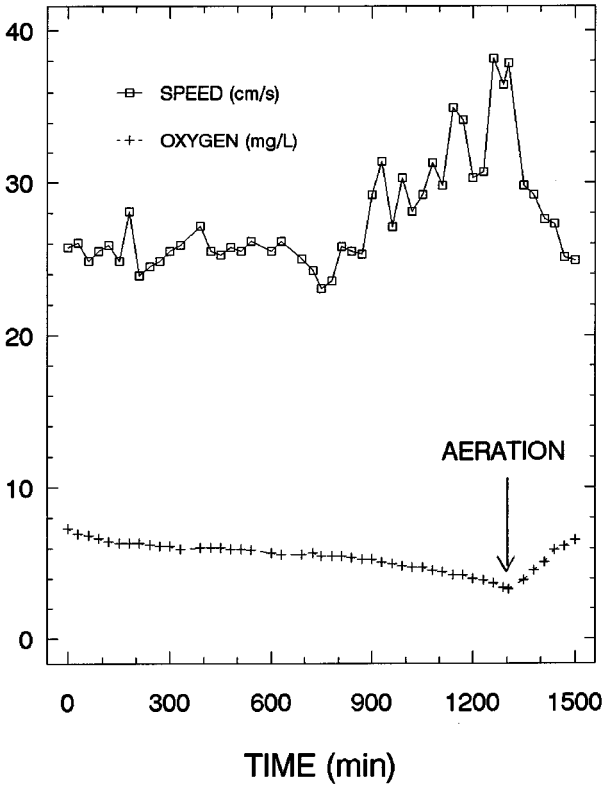

Figure 4. Changes in shark swimming speed and dissolved oxygen during a typical respirometry experiment.

Respirometry

Sharks (n = 7) ranging in size from 61.0 to 94.3 cm total length (mean = 77.4) were observed to increase swimming speed in response to decreasing dissolved oxygen. Data obtained demonstrated a relatively constant 25 cm s^{-1} swimming speed over about 6.5 to 5.5 mg l^{-1}. Between 4.5 and 5.4 mg l^{-1}, speed increased dramatically, reaching a maximum of about 38 cm s^{-1} at 2.0 to 3.0 mg l^{-1} (Figure 4). When aeration was begun in the respirometer, swimming speed decreased with increasing dissolved oxygen, and soon returned to pre-hypoxia values (5.5 to 6.5 mg l^{-1}). Repeated measures ANOVA indicated significant differences ($p = 0.0001$, df = 3) between all mean swimming speeds at all dissolved oxygen levels but no differences among sharks ($p = 0.9931$, df = 6).

We also found significant differences ($p = 0.0001$, df = 3) between mouth gape at all dissolved oxygen levels (Figure 5). Gape, measured at the symphyses of the palatoquadrates and Meckel's cartilages, increased from a normoxic value of about 1.0 cm maximum gape, to about 3.5 cm in hypoxic conditions. Similarly, increases in gape to dissolved oxygen levels were not different ($p = 0.9306$, df = 6) among sharks.

Weight specific respiration rate for 5 bonnethead sharks were significantly different ($p = 0.0177$, df = 3) between dissolved oxygen levels (Figure 5). Respiration rate at normoxia (6.0 mg l^{-1}) was about 115 mg O_2 kg^{-1} h^{-1} whereas respiration at hypoxia (3.0 mg l^{-1}) was about 350 mg O_2 kg^{-1} h^{-1}. Increases in respiration rate in response to dissolved oxygen levels were not different ($p = 0.0708$, df = 4) among sharks.

Gill ventilation volumes

We calculated gill ventilation volumes using the generalized equation:

$$Vg = \frac{r}{d.o.\ x\ e.e.} \qquad (1)$$

where, Vg is gill ventilation volume in liters h^{-1}, r is respiration rate in mg O_2 kg^{-1} h^{-1}, e.e. is extraction efficiency (the amount of oxygen removed from the water passing over the gills) and d.o. is dissolved oxygen in mg l^{-1}. Respiration rate (r) in the above equation was obtained from the relationship between respiration and dissolved oxygen (Figure 5). Substituting this into equation (1) provides:

$$Vg = \frac{1063.93 * (10^{-0.16lx})}{d.o. * e.e.} \qquad (2)$$

We calculated gill ventilation volumes using dissolved oxygen values ranging from 3.0 to 6.0 mg l^{-1} and extraction efficiencies of 25, 50 and 75% (Table 1). Ventilation volumes varied from about 467 l h^{-1} at 3.0 mg l^{-1} oxygen and 25% extraction efficiency to

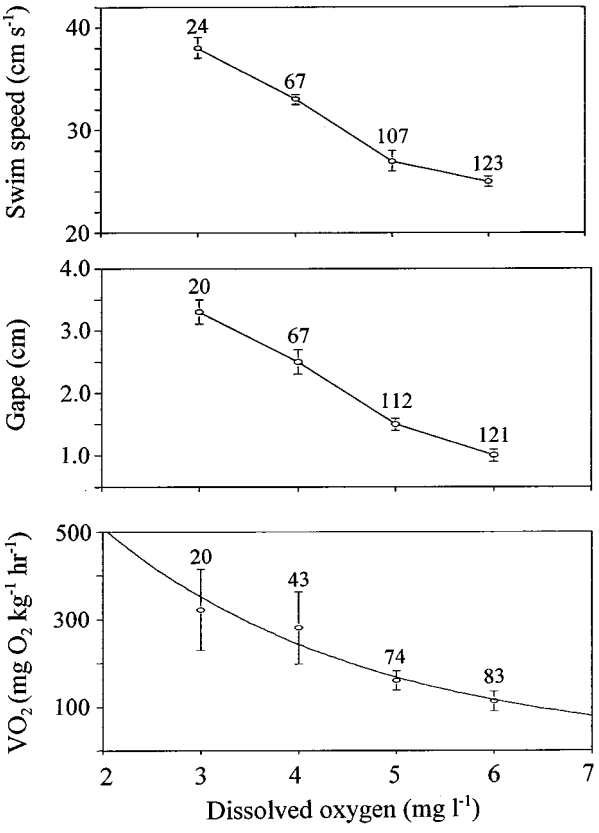

Figure 5. The effect of dissolved oxygen on swimming speed, gape and respiration rate. An exponential regression ($y = 1063.93*10^{-0.161x}$, $r^2 = 0.956$) was used to describe the relationship between dissolved oxygen and respiration rate. Numbers above each treatment indicate repeated measurements made on 5 to 7 individuals.

26 l h^{-1} at 6.0 mg l^{-1} and 75% extraction efficiency (Table 1).

Table 1. Dissolved oxygen and its effect on ventilation volumes. Ventilation volumes were calculated using equation (2) and extraction efficiencies (e.e.) of 25, 50 and 75%

Dissolved oxygen (mg l^{-1})	Ventilation volume (l h^{-1}) at e.e. of:		
	25%	50%	75%
3.0	467	233	156
4.0	241	121	80
5.0	133	67	44
6.0	77	38	26

Discussion

In situ *swimming speeds*

The sonic tag developed for this study allowed swimming speeds of untethered, captive sharks to be continuously recorded. After a period of acclimation, the tag appeared to have little or no effect on normal swimming speed. This was directly observable because *S. tiburo* prefer to swim in groups and the tagged shark spent most of the time swimming with two other untagged sharks in the lagoon. Additionally, Blaylock (1990) found that attachment of an external transmitter had no immediate effect on cownose ray, *Rhinoptera bonasus* swimming behavior. There was no trouble with the tag fouling because of the short time periods over which the tag was used. Although this tag was utilized in a controlled environment, it could be easily adapted for use on free-ranging sharks.

The results of this study suggest that *S. tiburo* maintains higher swimming speeds during nighttime activity. A nocturnal activity pattern has likewise been reported in the tiger shark, *Galeocerdo cuvieri* (Springer 1963), nurse shark, *Ginglymostoma cirratum* (Limbaugh 1963), horn shark, *Heterodontus francisci* and swell shark, *Cephaloscylium ventriosum* (Nelson and Johnson 1970) and lemon shark, *Negaprion brevirostris* (Gruber 1984; Gruber et al. 1988, Nixon and Gruber 1988). However, Hobson (1968) reported that *Carcharhinus* sp. are characterized by crepuscular feeding activities whereas Klimley et al. (1992) found no evidence for crepuscular feeding in the great white shark, *Carcharodon carcharias* at the South Farallon Islands, California.

The nocturnal activity pattern reported here is in contrast to earlier findings (Parsons 1991) which suggested that *S. tiburo* averaging about 75 cm total length maintain a relatively constant swimming speed of about 41 cm s^{-1}during day and night. In that study, swimming speeds were determined by an observer who estimated the time required for a shark to pass between two points. Individual sharks could not be identified so data from several similarly sized sharks were pooled. The use of the telemetry device in this study, provided continuously recorded swimming speeds for individual sharks. Possibly, the relatively crude method for determination of swimming speeds and the fact that individuals could not be identified may have masked any swimming speed differences in Parsons (1991). However, it is also possible that differences in diurnal oxygen concentrations observed

in this study could account for the swimming speed differences. The change in swimming speed observed in the present study coincided with diurnal changes in dissolved oxygen. Dissolved oxygen was observed to be at its lowest level in early morning (< 3.0 mg O_2 l^{-1}, 0500 h) and, after sunrise, increased steadily to a peak (6.0 mg $O_2 l^{-1}$) at 1600 h. Dissolved oxygen differences between the present study and that of Parsons (1991) may have been important in determining activity patterns. The lagoon in which sharks were studied in Parsons (1991) was aerated continuously to prevent changes in dissolved oxygen. The lack of a diurnal dissolved oxygen change in that study may explain the absence of a significant difference between night and day swimming speeds. This observation prompted us to examine the effect of hypoxia on swimming speeds under controlled conditions.

Hypoxia and its effect on swimming speed

There has been no work published on the effect of dissolved oxygen on swimming speeds in ram-ventilating sharks. However, this effect has been studied in ram-ventilating bony fishes. In some cases, the swimming speeds of ram-ventilating fishes may not vary with environmental change (Magnuson 1978) while in others there is an increase in speed (Dizon 1977). Gooding et al. (1981) found that sustained swimming in the skipjack tuna, *Katsuwonus pelamis* was independent of oxygen concentration until about 4.0 mg l^{-1}. Below this concentration, swimming speeds increased in a manner similar to that presented here. Bushnell and Brill (1991) report that both skipjack tuna, *K. pelamis* and yellowfin tuna, *Thunnus albacares* demonstrated increased swimming speed when dissolved oxygen declined to about 124 mmHg (about 6.0 mg l^{-1}). Swimming speed of a yellowfin tuna increased to about 60 to 65 cm s^{-1} at about 90 mmHg (about 4.3 mg l^{-1}). In this study, we observed increases in swimming speeds at about 5 mg l^{-1} and maximum speeds (about 40 cm s^{-1}) were observed at about 2-3 mg l^{-1}.

Swim speeds in the respirometer were somewhat greater than those observed *in situ* at similar dissolved oxygen concentrations. Similarly, Lowe (1996) found differences in swimming kinematics of scalloped hammerhead sharks, *S. lewini* between those swimming in a pond and those tested in a flume. We suggest that the differences in swimming speeds observed between sharks *in situ* and those in the laboratory may have been due to the added stress that resulted from handling and confinement in the respirometer.

It is interesting that tuna species apparently display a high sensitivity to hypoxia, responding to relatively modest decreases in dissolved oxygen concentrations. In contrast, *S. tiburo* did not show a measureable increase in swimming speed until about 5 mg l^{-1} dissolved oxygen likely due to the higher oxygen demand observed in tunas.

Hypoxia and its effect on mouth gape, respiration rate and ventilation volume

Typical fish are able to regulate gill ventilation by changing gill beat frequency, mouth gape, and, at least in some cases, swimming speed. It is also possible that branchial resistance to flow may be altered although we are not aware of this having been documented in fish. In the ram-ventilating fishes, an increase in swimming speed and/or an increase in gape are available for increasing gill ventilation rate. In this study we observed increasing mouth gape in response to hypoxia. This gaping behavior combined with the increase in swimming speed noted above, served to increase gill ventilation volume and thereby increase oxygen uptake.

We likewise recorded an increase in respiration rate with decreasing dissolved oxygen (Figure 5). This increase in respiration rate was likely indirectly related to hypoxia and probably due to increased swimming speeds and, thus, higher energy demands. This relationship illustrates an apparent contradiction in that oxygen uptake increases with decreasing oxygen availability. However, this is no different than other ventilatory regulating mechanisms such as increasing buccal pumping in typical fish or panting in birds or mammals. Although, there is a cost associated with each of these regulatory responses, the assumption with each is that the cost of increased ventilation is out-weighed by the benefit of increased oxygen uptake. The results presented here suggest that increased mouth gape and forward movement in response to hypoxia are important mechanisms for regulating gill ventilation and oxygen uptake.

The observed increase in respiration with decreasing dissolved oxygen also has important implications when closed system respirometry is used to determine routine metabolic rates for estimating daily energy budgets. If dissolved oxygen levels drop below about 5 mg l^{-1} then metabolic rates will be elevated resulting in inflated daily energy expenditure estimates.

When respiration rate and oxygen extraction efficiency are known then gill ventilation volume can be calculated (equation 2). We calculated gill ventilation volume (Table 1) over a range of dissolved oxygen values using observed respiration rates (Figure 5) and assumed extraction efficiencies. Extraction efficiencies in other elasmobranchs have been found to be about 25% in spiny dogfish, *Squalus suckleyi* (Lenfant and Johansen 1966) and about 50% in the dogfish, *Scyliorhinus stellaris* (Piper and Schumann 1967). Bushnell and Brill (1991) report about a 50% extraction efficiency in skipjack and yellowfin tuna. Although we report ventilation volumes across a range of extraction efficiencies, we suggest that due to its high activity levels, *S. tiburo* will have an extraction efficiency similar to *S. stellaris* of about 50%. Assuming this, ventilation volumes at normoxic conditions (5.0 to 6.0 mg l^{-1}) will be about 40 to 70 l h^{-1} (Table 1). This is in contrast to ventilation volumes measured by Bushnell and Brill (1991) for yellowfin and skipjack tuna using the dye dilution method. Under normoxic conditions (about 7.5 mg l^{-1}) yellowfin and skipjack tuna ventilation volumes were 486 and 612 l h^{-1}, respectively. We calculated ventilation volumes of these tuna species using equation (2) and values reported by Bushnell and Brill (1991, Table 2), and found good correspondence (421 and 594 l h^{-1}, respectively) with the dye dilution values. This suggests that reasonable ventilation volume estimates may be calculated using equation (2) when oxygen extraction efficiency and respiration rate are known.

We found it interesting that the tuna species have much higher ventilation volumes in comparison to *S. tiburo*. Parsons (1990) reports that *S. tiburo* has a metabolic rate similar to 'typical' bony fish whereas tuna species have elevated metabolic rates. Bushnell and Jones (1994) reviewed the various adaptations that support exceptionally high metabolic rates in tuna. Similarly, Brill (1996) considered the advantages of high performance physiology in tunas, bill fishes, and dolphin fish. Therefore, it is not surprising that ventilation volumes in fish with high metabolic rates such as tuna, would be different if extraction efficiencies are similar.

The above results suggest that swimming speeds of *S. tiburo* and of other ram-ventilating fishes may be affected by changing environmental oxygen concentrations. Parsons (1987) reports that during summer, dissolved oxygen concentrations measured on the grass flats in Florida Bay, Florida averaged 5 mg l^{-1}during the day. Concentrations at night would likely be lower. Although *S. tiburo* is a continuously active, ram ventilator its apparent tolerance to hypoxia may allow it to exploit the warm, shallow water environment more effectively than other shark species. If this is the case then it may be predicted that this species would demonstrate high blood oxygen affinity and a large Bohr factor similar to that seen in the hypoxia tolerant bat ray *Myliobatis californica* (Hopkins and Cech 1995). The results presented here suggest that dissolved oxygen must be considered in any study of swimming speed or metabolic rate in ram-ventilating fishes, in both a captive situation and in free-living animals.

Acknowledgments

The authors wish to express their sincere thanks to M. DeGruy, R. Smiley, M. Chan, J. Swanson, and the staff of the Florida Keys Regional Marine laboratory. Thanks are due to the staff of the National Marine Fisheries Service Laboratory in Panama City, Florida, in particular L. Trent. We also thank R. Holberton for reviewing the manuscript. Financial support for this project was supplied by the University of Mississippi, Office of Research, The Film Crew, The National Geographic Society and The National Marine Fisheries Service, Panama City, Laboratory. Special thanks are due S. Vargo and the Florida Institute of Oceanography.

References

Blaylock, R.A. 1990. Effects of external biotelemetry transmitters on behavior of the cownose ray, *Rhinoptera bonasus*. J. Exp. Mar. Biol. Ecol. 141: 213–220.

Brill, R.W. 1996. Selective advantages conferred by the high performance physiology of tunas, bill fishes, and dolphin fish. Comp. Biochem. Physiol. 113A: 3–15.

Bushnell, P.G. and Brill, R.W. 1991. Responses of swimming skipjack *Katsuwonus pelamis* and yellowfin *Thunnus albacares* tunas to acute hypoxia, and a model of their cardiovascular function. Physiol. Zool. 64: 787–811.

Bushnell, P.G. and Jones, D.R. 1994. Cardiovascular and respiratory physiology of tuna: adaptations for support of exceptionally high metabolic rates. Env. Biol. Fish. 40: 303- 318.

Dizon, A.E. 1977. Effect of dissolved oxygen concentration and salinity on swimming speed of two species of tunas. Fish. Bull. 75: 649–653.

Dizon, A.E., Neill, W.H. and Magnuson, J.J. 1977. Rapid temperature compensation of volitional swimming speeds and lethal temperatures in tropical tunas (Scombridae). Env. Biol. Fish. 2: 83–92.

Gooding, R.M., Neil, W.H. and Dizon, A.E. 1981. Respiration rates and low-oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*. Fish. Bull. 79: 31–48.

Gruber, S.H. 1984. Bioenergetics of the captive and free ranging lemon shark, *Negaprion brevirostris*. Ann. Proc. Am. Ass. of Zoological Parks and Aquariums. pp. 341–373. Wheeling, W. Virginia.

Gruber, S.H., Nelson, D.R. and Morissey, J. 1988. Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. Bull. Mar. Sci. 43: 61–77.

Hobson, E.S. 1968. Predatory behavior of some shore fishes in the Gulf of California. Fish. Bull. 72: 915–1031.

Hopkins, T.E. and Cech, J.J. 1995. Temperature effects on blood-oxygen equilibria in relation to movements of the bat ray, *Myliobatis californica* in Tomales Bay, California. Mar. Behav. Physiol. 24: 227–235.

Klimley, A.P., Anderson, S.D., Pyle, P. and Henderson, R.P. 1992. Spatiotemporal patterns of white shark, *Carcharodon carcharias* predation at the South Farallon Islands, California. Copeia 3: 680–690.

Lenfant, C. and Johansen, K. 1966. Respiratory function in the elasmobranch *Squalus suckleyi* G. Resp. Physiol. 1: 13–29.

Limbaugh, C. 1963. Field notes on sharks. *In* Sharks and Survival. pp. 63–64. Edited by P.W. Gilbert. D.C. Heath and Co., Boston.

Lowe, C.G. 1996. Kinematics and critical swimming speed of juvenile scalloped hammerhead sharks. J. Exp. Biol. 199: 2605–2610.

Magnuson, J.J. 1973. Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombrid and xiphoid fishes. Fish. Bull. 71: 337–356.

Magnuson, J.J. 1978. Locomotion by scombroid fishes: Hydromechanics, morphology, and behavior. *In* Fish Physiology. Vol. VII, pp. 239–313. Edited by W.S. Hoar and D.J. Randall. Academic Press, New York.

Metcalf, J.D. and Butler, P.J. 1984. Changes in activity and ventilation response to hypoxia in unrestrained, unoperated dogfish, *Scyliorhinus canicula* L. J. Exp. Biol. 108: 411–418.

Nelson, D.R. and Johnson, R.H. 1970. Diel activity rhythms in the nocturnal, bottom-dwelling sharks, *Heterodontus francisci* and *Cephaloscylium ventriosum*. Copeia 4: 732–739.

Nixon, A.J. and Gruber, S.H. 1988. Diel metabolic activity patterns of the lemon shark, *Negaprion brevirostris*. J. Exp. Zool. 248: 1–6.

Parsons, G.R. 1987. Life History and Bioenergetics of the Bonnethead Shark, *Sphyrna tiburo* (Linnaeus): A Comparison of Two Populations. Ph.D. Dissertation, University of South Florida at St. Petersburg, USA.

Parsons, G.R. 1990. Metabolism and swimming efficiency of the bonnethead shark, *Sphyrna tiburo*. Mar. Biol. 104: 363–367.

Parsons, G.R. 1991. Activity patterns of the bonnethead, *Sphyrna tiburo*. J. Aquaricult. Aquat. Sci. 4: 8–13.

Piper, J and Schumann, D. 1967. Efficiency of oxygen exchange in the gills of the dogfish, *Scyliorhinus stellaris*. Resp. Physiol. 2: 135–148.

Randall, D.J. 1970. The circulatory system. *In* Fish Physiology. Vol. IV, pp. 133–168. Edited by W.S. Hoar and D.J. Randall, Academic Press, NewYork.

Smit, H., Amelink-Koutstaal, J.M., Vijverberg, J. and von Vaupel-Klein, J.C. 1971. Oxygen consumption and efficiency of swimming goldfish. Comp. Biochem. Physiol. 39A: 1–28.

Springer, S. 1963. Field observations of large sharks of the Florida-Caribbean region. *In* Sharks and Survival. pp. 95–114. Edited by P.W. Gilbert. D.C. Heath and Co., Boston.